

SNOWSHOE HARE DENSITIES IN POST-FIRE VEGETATION

By

Hans Mathias Eriksson

RECOMMENDED:

John Hilland
Scott Rupp
[Signature]
Advisory Committee Chair

Edward C. May
Assistant Chair, Department of Biology and Wildlife

APPROVED:

[Signature]
Dean, College of Natural Science and Mathematics

[Signature]
Dean of the Graduate School

April 25, 2006
Date

SNOWSHOE HARE DENSITIES IN POST-FIRE VEGETATION

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Hans Mathias Eriksson, Cand. Mag.

Fairbanks, Alaska

May 2006

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Abstract

The objective of this study was to investigate if patterns of snowshoe hare (*Lepus americanus*) densities in interior Alaska are influenced by post-fire successional stage. Stages of succession were classified using the proxy Time Since Last Fire (TSLF). I estimated snowshoe hare densities during the summers of 2003 and 2004 in 5 young (10-20 yrs) and 5 old (44-46 yrs) burns, each with an adjacent unburned control, using indirect distance sampling methods. Because indirect distance sampling has not previously been applied for snowshoe hares, I compared these results with a traditional mark-recapture analysis. Hare density estimates from both methods were not statistically different. I observed that hare densities were not higher in older stands relative to unburned habitat and that hare densities were highly variable in young stands. Therefore, my research suggests that TSLF was not suitable as a stand-alone indicator of quality of habitat for snowshoe hares. Other processes and factors such as fire severity can influence successional pathways and post-fire species composition, creating both temporal and spatial variability in the development of successional stages. I recommend that other covariates, such as fire severity, be researched to address the influence of vegetation succession on hare densities.

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Acknowledgements

This study was supported in part by the Bonanza Creek Long-Term Ecological Research program. My graduate committee, Eric Rexstad, Knut Kielland and Scott Rupp, provided help and guidance during the course of this project. Thank you. I am also very grateful to my friends and volunteers, Andrea Croll, Emil Eriksson, Mattias Augustsson and Anders Waller for help and support in the field. This document has been improved by comments from my private editor and wife Andrea Croll.

General Introduction

Snowshoe hares (*Lepus americanus*) are ubiquitous in the boreal forest of North America. Their numbers fluctuate dramatically over an 8-11 year cycle (Keith and Windberg 1978; Keith 1990), and many ecosystem processes respond to these oscillations. When at peak densities, snowshoe hares may affect both vegetation dynamics (Grange 1965; Bryant and Chapin 1986; Bryant 1987; Bryant et al. 1994) and biogeochemical processes (Kielland et al. 1997; Ruess et al. 1998) through heavy browsing.

Wildfire has been proposed as a driving factor of the hare cycle (Grange 1965; Fox 1978). Early hypotheses about the snowshoe hare cycle argued that fire-associated plant succession has an important role during the population growth phase of the hare cycle (Grange 1965). Even though hares are found in most stages of northern forest development, their potential for high density, as seen at the cyclic peak, is confined to early successional stands (Grange 1965). This is because high quality food is abundant in early stages of succession (Grange 1949; Wolff 1980).

Wildfire is the primary initiator of secondary succession in interior Alaska (Vioreck 1973) and burns on average approximately 270 000 hectares of forest annually across the state (Kasischke et al. 2006). Fires that have burned over time create a landscape mosaic with patches of vegetation at different successional stages

Fox (1978), identified a strong correlation between the cyclic patterns of large fire years and lynx fur returns. This indicates, based on the strong predator-prey linkage between lynx on snowshoe hares, that the amount of area burned could drive the snowshoe hare cycle (Fox 1978). The rationale followed Grange's (1965) explanation that hare numbers are driven by fire-associated plant succession. Therefore, a cyclic pattern in area burned would generate a corresponding pattern in the potential for high hare densities through a cyclic abundance of young successional vegetation.

I was interested in knowing how snowshoe hares might respond to the habitat mosaic that characterizes the boreal forest of interior Alaska. The objective of this study was to evaluate if burns at different post-fire successional stages influence snowshoe hare densities during the summer. I predicted, based on Grange (1965) and Fox (1978), that young burns (10 to 20 yrs) would have a relatively higher hare density compared to old burns (44 to 46 yrs) or unburned habitat because of a more abundant food supply. I also predicted that hare densities would be similar between old burns and unburned habitat because vegetation characteristics important to snowshoe hares should be similar between the 2 habitats.

Abstract

The objective of this study was to investigate if patterns of snowshoe hare (*Lepus americanus*) densities in interior Alaska are influenced by post-fire successional stage. Stages of succession were classified using the proxy Time Since Last Fire (TSLF). I estimated snowshoe hare densities during the summers of 2003 and 2004 in 5 young (10-20 yrs) and 5 old (44-46 yrs) burns, each with an adjacent unburned control, using indirect distance sampling methods. Because indirect distance sampling has not previously been applied for snowshoe hares, I compared these results with a traditional mark-recapture analysis. Hare density estimates from both methods were not statistically different. I observed that hare densities were not higher in older stands relative to unburned habitat and that hare densities were highly variable in young stands. Therefore, my research suggests that TSLF was not suitable as a stand-alone indicator of quality of habitat for snowshoe hares. Other processes and factors such as fire severity can influence successional pathways and post-fire species composition, creating both temporal and spatial variability in the development of successional stages. I recommend that other covariates, such as fire severity, be researched to address the influence of vegetation succession on hare densities.

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Wildfire has been proposed as a driving factor of the hare cycle (Grange 1965; Fox 1978). Early hypotheses about the snowshoe hare cycle argued that fire-associated plant succession has an important role during the population growth phase of the hare cycle (Grange 1965). Even though hares are found in most stages of northern forest development, their potential for high density, as seen at the cyclic peak, is confined to early successional stands (Grange 1965). This is because high quality food is abundant in early stages of succession (Grange 1949; Wolff 1980).

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¹ Prepared for publication in the Canadian Journal of Zoology. Authors: H.M. Eriksson, E. Rexstad, K. Kielland.

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Snowshoe hares utilize a patchy landscape with preferred habitat types, ranging from dense mature forest to young successional stands, depending on seasonal need in diet and protection (Wolff 1980). Open herbaceous areas, typical of young successional stands, containing high quality foods are used in the summer. Older stands, like mature black spruce, where browse is scarce (Keith et al. 1984) but escape cover is good, are used during the winter months and cyclic population lows (Wolff 1980).

The potential for high hare density in a successional stand diminishes with time (Grange 1965) as vegetation grows beyond the reach of hares. Not only food availability changes as succession progresses, but other vegetation characteristics important to hares, like understory vegetation density (Adams

1959; Meslow and Keith 1968; Wolff 1980; Wolfe et al. 1982; Litvaitis et al. 1985; Wirsing et al. 2002) and canopy cover (Litvaitis et al. 1985), change as well. Changes in plant community, such as species composition and vegetation vertical structure, also could influence hare density. Because these vegetation characteristics change with succession, Time Since Last Fire (TSLF), used as a proxy for succession, may influence relative patterns of hare density at the landscape scale.

I was interested in knowing how snowshoe hares might respond to the habitat mosaic that characterizes the boreal forest of interior Alaska. The objective of this study was to evaluate if burns at different post-fire successional stages influence snowshoe hare densities during the summer. I predicted, based on Grange (1965) and Fox (1978), that young burns (10 to 20 yrs) would have a relatively higher hare density compared to old burns (44 to 46 yrs) or unburned habitat because of a more abundant food supply. I also predicted that hare densities would be similar between old burns and unburned habitat because vegetation characteristics important to snowshoe hares should be similar between the 2 habitats.

Methods

Direct estimation of snowshoe hare density using distance sampling can be problematic because (1) hares most likely have a low detection probability in dense vegetation; (2) hares exhibit behavioral avoidance of the person sampling;

(3) accurate distance measurements are hard to achieve at high and low population densities; (4) considerable sampling effort is required at low population densities (Newey et al. 2003).

Estimating snowshoe hare densities on a landscape scale by direct estimation methods such as mark-recapture was not feasible because it would have been too labor intensive. Indirect methods such as the pellet plot count, (Krebs et al. 1986; Krebs et al. 2001; Murray et al. 2002) or indirect distance sampling, (Plumtre 2000; Buckland et al. 2001; Marques et al. 2001) are used as alternatives. Both methods are labor and cost efficient, which allows for large sample sizes and more replication than a mark-recapture approach.

I used Indirect distance sampling in this study in preference over pellet plot counts because (1) I only required a single survey per study area to estimate hare density; whereas for a pellet plot study it is recommended that areas be cleared of pellets 1 year prior to the census (Krebs et al. 1987; Murray 2005), and (2) distance sampling is a plotless method that does not require plot or area measurements to estimate hare density. This feature has the benefit of avoiding issues related to the size and shape of the sample plot, which may influence the relationship between pellet counts and hare density estimates (Krebs et al. 1987, Krebs et al. 2001; Murray et al. 2002). Indirect distance sampling produces an index of hare density (i.e., pellet group density) similar to that of pellet plot counts. To convert this index to actual hare density estimates, the accurate estimates of snowshoe hare fecal decomposition and defecation rates are required.

I used a study design based on a natural experiment, using TSLF as a treatment and 2 treatment levels, young burns (TSLF of 10-20 years) and old burns (TSLF of 44-46 yrs). The choice of thresholds for each TSLF class was determined based on (1) accessibility to burned areas; (2) the observation period of the fire history database (1950-2003) (Bureau of Land Management Alaska; Alaska fire perimeter dataset, available from <http://agdc.usgs.gov/data/blm/fire/index.html>) and (3) burns 1 to 4 years old were not included because they are known to be avoided by hares (Wolff 1980).

I used a matched pair design to reduce the effect of extraneous variation, in which each treatment area was paired with an adjacent unburned control. I assumed, based on proximity to the burn, that each control/burn pair shared similar pre-fire habitat characteristics. I included 5 replicates per treatment level pair to provide inferential value at the landscape scale (Figure 1; Table 1).

Distance sampling

I sampled snowshoe hare fecal pellet groups during the summers of 2003 and 2004 following green-up. I established 100 meter transects spaced 200 meters apart. Transects were placed systematically using a random starting point at least 100 meters from the edge of the burn or from any road to prevent edge effects. Following Buckland et al.'s (2001) recommendations on sample size, I sampled at least 10 transects in each study site to provide sufficient area

coverage with a minimum of 60 detected objects (e.g., fecal pellet groups) per site to provide enough data for model fitting.

I only sampled summer pellets to keep the inference of the study to the summer season. To avoid dependence between detections I used snowshoe hare pellet groups instead of individual pellets as the sampling unit. Pellet groups were detected on both sides of each transect and the perpendicular distance from the transect to the center of each pellet group was measured. Snowshoe hares appeared to defecate primarily in diffuse pellet groups (approx. radius > 30 cm). This sometimes caused problems identifying the center point of a pellet group. There was also risk of double counting if the hare had been defecating while running parallel to the transect. This could create many small pellet groups along the transect line, all from 1 defecation event. Therefore, I only recorded the first pellet detected to avoid double counting. When I did not detect the whole pellet group instantaneously, I used the center of the initially detected pellet group to measure the perpendicular distance.

Vegetation Sampling

Vegetation measurements included (1) canopy cover and (2) proportion ground cover of hare browse items. The latter was composed of 2 samples, one from the understory and one from the ground cover vegetation. All vegetation measurements were recorded during the summer of 2004 using a GRS densitometer (Geographic Resource Solutions, Arcata, CA). Vegetation sampling

was conducted immediately after the pellet distance sampling along the same transect centerline. Observations from the 3 measurement categories were recorded every 10 paces along the transect with an average of 12 observations per transect line. I recorded measurements of canopy cover and understory about 0.5 m above the ground to approximate the snowshoe hares' perspective. I recorded the ground cover data standing up and looking down through the densitometer.

Plant species that composed the majority of the snowshoe hare's summer diet (Wolff 1978) were identified for ground cover of browse items. These species included *Salix* spp., *Betula* spp., *Ledum groenlandicum*, *Vaccinium* spp., and *Equisetum* spp.

The summer of 2004 was a record fire year and large areas burned throughout interior Alaska, including the study sites at Steese, Central and CHRD 58. Hence, there are no data on vegetation and hare densities from these sites for the 2004 season.

Fecal Decomposition and Deposition Rate

Estimated pellet group density is converted to hare density by division by pellet group decomposition and deposition rate. The fecal pellet group density observed in the field is a result of the accumulation rate of pellet groups due to defecation minus the average rate at which the pellet groups disappear (Buckland et al. 2001; Marques et al. 2001). Decomposition and defecation rate

vary with time and space and are not always easy to estimate. Fecal pellet decay rate varies with habitat (Cochran and Stains 1961; Lehmkuhl et al. 1994; Massei et al. 1998; Prugh and Krebs 2004), and physical factors associated with habitat and season, such as moisture (Murray et al. 2005) and temperature (Cochran and Stains 1961). Mayle and Peace (1999) found that decay rate of pellet groups is negatively correlated with moisture and positively correlated with temperature. They also noted, however, that the single strongest influence on decay rate was a negative correlation with an index of evaporation, which combines the effects of humidity and temperature.

The interior Alaska summer climate is usually warm and dry early in the season with mean June temperature of 14°C and average total precipitation of 16 mm. July mean temperature is 15°C and average total precipitation is 30 mm. August is usually wetter with an average total precipitation of 42 mm and a mean temperature of 12 °C (National Climate Center: <http://climate.gi.alaska.edu>; climate norms from 1971-2000 - Division 8 interior Alaska).

Fresh hare pellets collected in June 2003 and 2004 from hares caught in live traps at Bonanza Creek Experimental Forest (BCEF) were used to estimate year-specific decomposition rates. To incorporate some habitat dependent variability into the decomposition rate estimates, pellets were placed in 4 different habitat types at BCEF: black spruce (*Picea mariana*) forest, mixed black spruce and birch (*Betula spp.*) forest with dense understory, wet mixed black spruce, aspen (*Populus tremuloides*) and alder (*Alnus crispa*) forest and dry deciduous

birch, willow (*Salix spp.*) and aspen forest. Three marking sticks were placed randomly in each habitat type and 3 pellet groups were placed at randomly selected cardinal directions around each stick. Pellets were placed in groups of 4, 5 and 6 pellets, which bracketed the average group size encountered in the field. Sites were revisited approximately once a week and remaining pellet groups were recorded. A pellet group was deemed decomposed when only 1 pellet remained.

While moisture and temperature vary by habitat locally, similar habitats might vary in moisture and temperature at the landscape scale depending on regional meteorological differences. Decay rate was measured at 1 locale, BCEF, but pellet group densities were measured at 20 sites across the study area. It was therefore necessary to determine whether factors influencing decay rate were similar across the study area.

I used the Fine Fuel Moisture Code (FFMC), a component of the Canadian Fire Weather Index (FWI) (Van Wagner 1987), as an indicator of meteorological conditions to investigate if the fuel moisture of the upper soil layer, and hence conditions for pellet decay, were similar throughout the study area. The Alaska Fire Service (AFS) collects FFMC data from weather stations across interior Alaska.

I used FFMC data from the Fairbanks weather station (Table 3), which was 2 km from the decay experiment site to indicate meteorological factors at that site. The summer average FFMC data from the Fairbanks weather station

was then compared to other FFMC stations in the interior; 8 FFMC stations in 2003 and 10 stations in 2004 (Table 3). The software SAS (SAS Institute Inc., Version 8, Cary, NC) was used to investigate normality of FFMC measures within each station, and after that an ANOVA on the ranked daily FFMC values was used to test if the meteorological stations differed from each other within each year. If the ANOVA was significant, a Tukey type multiple comparison was used to determine which weather stations differed from the Fairbanks weather station in average FFMC.

There are many reports on individual pellet defecation rates for snowshoe hares in the literature but none on defecation rates of pellet groups. Hirakawa and Okada (1995) presented information on pellet group defecation rates for 3 Japanese hares (*Lepus brachyurus*) fed on commercial food, which served as estimates for snowshoe hare defecation rates in this project.

Hare Density Validation

In August 2003 and 2004, I collected both pellet group distance and mark-recapture data at BCEF outside of Fairbanks where a snowshoe hare mark-recapture study was ongoing. Handling of hares was in accordance with guidelines (Canadian Council on Animal Care 1984) and was approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee. I analyzed the trapping data using inverse prediction methods (Efford 2004) with the software program DENSITY

(<http://www.landcareresearch.co.nz/services/software/density>). I compared the direct estimates of hare density derived from inverse prediction with the indirect estimates derived from distance sampling using 95% confidence intervals.

Distance Data Analysis

I analyzed pellet group data with the software program DISTANCE (Thomas et al. 2004). All analyses were run with a 10% truncation filter to eliminate model over-fitting at the tail of the detection function. As standard during the modeling of the detection function, all detection probability histograms were fitted with the half normal, uniform, and hazard rate detection functions. Competing models, within 2 Akaike's Information Criterion (AIC) units of the best model, were also run with the available adjustment terms. Only in cases where the histograms showed a typical negative exponential shape did I try to fit that function. AIC was used to select the model that fitted the data best. The resulting model with the lowest AIC was examined for goodness of fit and convergence. I compared hare pellet group densities, adjusted for pellet deposition and decomposition between burned and unburned areas within each site using a Z-test as outlined by Buckland et al. (2001, page 353). This test is recommended for comparisons of densities when sample sizes are large (>30).

To examine the influence of fire on hare densities at a landscape scale I used a meta-analysis approach (Rexstad and Anderson 1988). I used the within-site difference, \hat{d}_i , in hare density between burn and control as the response

variable, where the subscript i indicates site. The response variable was weighted with the inverse of the variance $\text{var}(\hat{d}_i)$. The weighted differences were averaged within each treatment level, \bar{d}_y and \bar{d}_o , and their variance, $\text{var}(\bar{d}_y)$ and $\text{var}(\bar{d}_o)$, calculated. Subscripts y and o define young and old sites respectively. I compared the weighted treatment level means with a Z-test to investigate if TSLF influenced snowshoe hare density. The prediction is $\bar{d}_y > \bar{d}_o$ (i.e., there is on average a greater density of snowshoe hares in young burns compared with old burns).

Results

Vegetation Structure

Many of the observed differences in percent canopy cover and browse item ground cover between burn and control were significant (Figure 2, Table 2). The canopy cover in 2 out of 4 young sites (Yukon North and Yukon Middle) were consistent with the prediction that young burns have a less dense canopy cover than a unburned area (Figure 2). In contrast, the Yukon South site, also a young burn, had a significantly denser canopy cover than the control. Canopy cover estimates in the old sites ($n = 3$) were similar between burn and control, as expected, but there were 2 exceptions. At Healy and O'Brien Creek, estimates of canopy cover were significantly higher in the control compared with the burn.

The pattern of browse availability was similar between burn and control was similar in young and old sites. The proportions of browse were significantly higher in the burn compared to the control at Yukon North, Yukon South and CHRD 59. However, the proportion of browse items was significantly higher in the control compared to the burn at O'Brien Creek (Figure 2). These results support the predictions that browse availability is higher in young burns than controls, but that browse availability is no different between old burns and controls.

Fecal Decomposition Rates

The mean FFMC indicated dryer conditions in 2004 than in 2003 (Table 3), which reflects the severe fire year of 2004. The nonparametric ANOVA comparing average FFMC across stations was significant in both years (2003: $F_{7,684} = 6.2$, $P < 0.0001$; 2004: $F_{9,890} = 9.09$, $P < 0.0001$). The FFMC at the Fairbanks station was similar to all the other stations in 2003, although in 2004 the Nenana station, 1 out of 9 stations, had a significantly lower mean FFMC.

The mean time of pellet group decomposition was 48 ± 3 days in 2003 and 65 ± 4 days in 2004. The faster decomposition in 2003 is reflected in the fuel moisture data, which shows the 2004 season was dryer.

Hare Density Validation

Hare density estimated using distance sampling was 1.3 ± 0.3 hares/ha in 2003 while the mark-recapture density estimate was 0.8 ± 0.3 hares/ha. The 2004 density estimates showed less difference with 0.9 ± 0.2 and 0.8 ± 0.3 hares/ha estimated from distance sampling and mark-recapture techniques, respectively. There was no significant difference between the density estimates produced from distance and mark-recapture techniques in either year (Figure 3).

Hare Densities

Snowshoe hare densities across treatments ranged from 0.2 to 3.2 hares/ha in 2003. The hare density estimates in 2004 ranged from 0.1 to 1.9 hares/ha (Figure 4). The consistently higher density estimates in 2003 compared to 2004 possibly resulted from misclassification of some winter pellets as summer pellets in the first field season. More rigor was used to correctly identify summer pellets in the 2004 survey. A correlation between 2003 and 2004 hare densities shows a strong relationship between the 2 seasons ($r^2 = 0.9763$) and indicates that the overestimation of hare density in 2003 was consistent across burned and unburned areas. Because the emphasis of this study is on the difference in hare density between treatments, the overestimation of hare density in 2003 did not affect the analysis.

I found no significant differences in hare densities between old burns and the controls (Figure 5), which matches the prediction that fires older than 40

years are similar to unburned forest from the vantage point of snowshoe hares. As expected for a young burn, hare densities were significantly higher in the burn at Yukon South for both years. In contrast to the prediction, hare densities at Yukon North were significantly higher in the control in 2004 but not in 2003. Unexpectedly, all other differences in hare density between the young burns and controls were non-significant.

The differences in canopy cover and browse items between burn and unburned areas when juxtaposed with the differences in hare densities for the same sites did not explain the observed pattern of hare densities between burn and control.

Meta-analysis

In 2003, the analysis indicated that densities of hares averaged higher in burns than controls for both young and old burns. The difference was greater in the young sites than in the old sites where the mean difference was close to zero. However, when mean differences in hare density were compared across treatment levels, no difference between young and old burns could be detected (2003: $\bar{d}_y = 0.257$; $\hat{\sigma}_y^2 = 0.065$; $\bar{d}_o = 0.032$; $\hat{\sigma}_o^2 = 0.006$; $P = 0.205$; 2004: $\bar{d}_y = -0.234$; $\hat{\sigma}_y^2 = 0.048$; $\bar{d}_o = 0.053$; $\hat{\sigma}_o^2 = 0.004$; $P = 0.103$) (Table 4). It is worth noting that the difference in hare density for young sites Yukon South and Rosie Creek in 2003 was about equal in magnitude, but opposite in direction. The average differences in hare density between old burns and controls were similar in 2003

($\bar{d}_o=0.032$) and 2004 ($\bar{d}_o=0.053$). The average differences of hare density between young burns and controls, however, indicated that there were relatively more hares in the burn in 2003 ($\bar{d}_y=0.257$) but more hares in the control in 2004 ($\bar{d}_y=-0.234$).

Due to large variance in hare density estimates, I conducted a sensitivity analysis to investigate whether better precision could have changed the results of the meta-analysis. A 90% reduction in the variance of old burns did not produce a significant test statistic in either year. A similar reduction in the variance of the young burns in 2003 produced a significant difference in relative hare density between young and old burns. In 2004, a 70% reduction in the variance of young burns was enough to produce a statistical treatment effect. The large reductions in hare density variance required to effect a change in the results of the analysis indicate that imprecision in any single facet of the analysis was insufficient to overturn my overall results. Only large changes in the precision of the estimates could have changed my findings.

Discussion

Hare Density Validation

The snowshoe hare population in interior Alaska was in a cyclic low in 2003 and 2004 (Unpublished data 2006, data accessible through the LTER data library at <http://www.lter.uaf.edu>). The hare density estimates from this study, except for CHRD 58 and 59, are higher than for most other cyclic low estimates

of hare density from other parts of the northern boreal forest (Table 6.1 in Hodges 2000a). However, Murray et al. (2002) reported snowshoe hare density estimates of up to 2.12 hares/ha from low-density populations, which is in the range of hare density estimates from this study (2004: 0.2 to 2.5 hares/ha).

A comparison of sampling methods showed no significant difference between the indirect and the direct sampling strategies. These results indicate that distance sampling of fecal pellet groups can be as effective as mark-recapture methods in estimating hare density, as long as summer pellet groups are identified correctly.

Fecal Decomposition Rate

One could argue that the approach of estimating decomposition rate of pellet groups used in this study may produce biased or imprecise estimates if decomposition rates are dependent on season, pellet group size, and/or age (Marques et al. 2001; Laing et al. 2003). The fact that I sampled only summer pellets should have limited the seasonal influence on decay rate because the majority of snowshoe hare summer pellets decompose over the summer (Murray et al. 2005). Although the average FFMC of some weather stations other than the Fairbanks station differed statistically from one another, the overall similarity to the Fairbanks station indicated that meteorological conditions were similar across the study area and should not have a large impact on decay rates throughout both field seasons.

The variance of the estimated mean time to disappear might be underestimated because the pellet group sizes used in the decay experiment did not reflect the complete range of pellet group sizes in the field. However, hare density variance was robust to decay rate variability because of the relatively low contribution of decay rate to hare density variance, 2% to 16% depending on the site and year (Table 5). Given the high variation in hare density estimates from encounter rate and detection probability, any under or overestimation of decay rate variability likely did not affect the results of this study.

Fecal Deposition Rate

Fecal deposition rate for lagomorphs, just as decomposition rate, has the potential to differ among seasons (Wolff 1978), geographic region (Hodges 2000a; 2000b) and diet (Cochran and Stains 1961; Murray et al. 2005). Murray et al. (2005) noted different pellet production rates for snowshoe hares on 11 different winter diets but, when scaled to consumption rate, pellet production was not statistically significant among diets.

I compared the laboratory defecation rates between snowshoe hares (Sinclair et al. 1982) and Japanese hares (Hirakawa and Okada 1995) to guard against potential differences in deposition rate between the 2 species. Deposition rates of both species were based on diets with similar crude protein content, which are comparable to that of wild snowshoe hares during the summer months, 18% to 22% (Sinclair et al. 1982). I assumed that Japanese hares had similar

fecal pellet water content as mountain hares (*Lepus timidus*) (Pehrson 1983) when converting wet fecal weights from Japanese hares to dry fecal weights.

Snowshoe hares deposit approximately 0.30 g of dry feces/g of dry food while Japanese hares deposit approximately 0.35 g dry feces/g dry food. Having a similar dry feces deposition rate, however, is not the same as having a similar number of defecation events in one day. Yet it still shows that Japanese hares and snowshoe hares are similar in 1 regard, gram of dry feces deposited per gram of dry food consumed, related to the number of defecation events per day.

Meta-analysis

There was no evidence that hare densities were higher in young burns in interior Alaska, on average, than in controls or old burns. That is to say, quantitatively there was no treatment level effect. Qualitatively, the results in Figure 5 indicate that from the perspective of snowshoe hares, 50-year-old burns have returned to a mature forest with little evidence of burning. According to both the vegetation data and the hare densities, young burns are still different from paired controls and, at times, associated with higher snowshoe hare densities, as in the Yukon South burn. On the other hand, the higher hare density in the control at Yukon North in 2004 cannot be explained from the vegetation data. From a subjective point of view based on reported importance of understory cover in hare habitat (Adams 1959; Meslow and Keith 1968; Wolff 1980; Wolfe et al. 1982; Wirsing et al. 2002), a burn like Yukon North with few patches of dense

brush isolated by large spaces of grass and dead trees is not a good snowshoe hare habitat.

In this study, canopy cover and browse availability had little explanatory power on hare density. Compared with their respective paired areas, canopy cover was significantly higher at the Yukon South burn and the Yukon North control, where hare densities were also significantly higher. However, other areas (e.g., Yukon Middle and Healy controls) with significantly higher canopy cover did not have higher hare densities. Browse availability was higher in most burns of both age classes relative to their controls, but as with canopy cover, browse availability did not help explain the observed pattern of hare density estimates. For example, the higher browse availability at Yukon South was in accordance with the higher hare density, as expected, but the hare density in Yukon North in 2004 was opposite to that prediction.

Of all the young sites sampled in this study, only Yukon South was in accordance with all of the predictions. In both years, there were higher hare densities in the burn, as well as significantly higher canopy cover and browse availability. This site was unique, however, in that dense, tall willow dominated the brush layer. The tall willow brushes registered on the densitometer and constituted a large part of the estimated canopy cover as well as that of the browse availability estimate. Willow is the preferred browse species of snowshoe hares during the summer (Wolff 1978), and, so in combination with the dense understory, the Yukon South burn was good hare habitat. Other sites had equally

large or larger estimates of hare densities, canopy cover, or browse availability associated with them but Yukon South was the only site that had all of these characteristics (Figure 4; Table 2).

The browse availability data from this study does not support Grange's (1965) hypothesis that areas with abundant high quality food should contain high hare densities. There are 2 interpretations why browse availability did not help explain differences in hare densities. First, the browse availability measurements did not take relative preference of browse species into account. Although 2 estimates of browse availability might be identical numerically, they are most likely comprised of different species compositions, and so their influence on snowshoe hares would depend on the proportion of highly preferred browse species in each estimate. For example, if the majority of species making up the browse availability estimate were of medium preference to hares, the influence of browse availability could have been overestimated. Second, even though snowshoe hares and other mammals are attracted to areas with abundant food (Hodges et al. 2001), food availability is not the only factor dictating the hare cycle. Predation pressure in simultaneous interaction with food availability has been demonstrated to affect hare demography to a greater extent than food availability alone (Hodges et al. 2001). Hodges et al. (2001) also showed that food addition can significantly increase peak population densities of snowshoe hares. However, food addition experiments conducted during the cyclic low phase resulted in only small population increases (Hodges et al. 2001).

Therefore, other factors, like predator escape cover, may have a more important influence on hare density at the cyclic low phase than food availability.

Performance of Indirect Distance Sampling

Though the variances associated with the indirect distance sampling estimates were similar to those of the mark-recapture estimates (Figure 3), an improvement of the precision of the indirect distance method could increase the power of this method and allow for detection of smaller differences in hare densities.

The meta-analysis was not sensitive to artificial reductions in variance, but a 70% reduction of the group variance for the young burns did change the outcome of the Z-test. The group variances in the meta-analysis are composites of variances from the plot hare densities. The variance associated with each plot density estimate is in turn composed from 4 sources of variation: detection probability, encounter rate, pellet decay, and pellet deposition. Of these, encounter rate is by far the principal contributor to the variance in hare density, comprising approximately 35 to 85% of the variance (Table 5). This is consistent with Buckland et al. (2001), who stated that encounter rate variance is often the major contributor to density variance.

Any effort to improve the performance of the indirect distance method as used in this study should first focus on reducing the encounter rate variance.

Snowshoe hare pellets exhibit a clustered distribution, with most pellets found in

areas used for foraging (Murray et al. 2005) and few pellets found in open areas that hares essentially avoid. Based on this information, stratifying sampling transects by habitat should result in reduced encounter rate variance. Understory density has been shown to correlate with snowshoe hare numbers (Adams 1959; Meslow and Keith 1968; Wirsing et al. 2002) and should be useful as a stratification metric. Choosing the appropriate transect length or placing transects relative to proximate factors of hare density, like understory density, can reduce the number of transects with zero encounters. Apart from methodological improvements in the sampling design, a set of covariates with more explanatory power could have been more enlightening. Again, density of understory vegetation is likely to do a better job as a covariate with TSLF than canopy cover.

Grange (1965) estimated that the time lag between a fire and potential hare peak density is 6-13 years. This was supported by Fox's (1978) correlation between annual area burned and hare abundance, but Fox also noted that a second correlation between age of burn and peak hare density existed between 15-22 years post-fire. Both the 6-13 and 15-22 year time lags correlate with the peak of the 8-11 year hare cycle and show support for Grange's hypothesis of a fire driven hare cycle. Even though all of the young burns in this study were within Grange's (1965) and Fox's (1978) estimated time lags, my data suggested that the hare cycle was at a cyclic low. Considering that the snowshoe hare population at BCEF in 2005 indicated that a cyclic increase phase had begun (Unpublished data 2006, data accessible through the LTER data library at

<http://www.lter.uaf.edu>) the estimated time lag between fire and hare density of Grange (1965) and Fox (1978) might still hold.

The results from this study indicate that young burns in contrast to old burns are more variable in their influence on hares. It is possible that many of the burns included in the young age category had either not yet developed the vegetation structure that influence hare density, or had passed the successional stage where they are attractive to hares.

I used TSLF as a proxy for vegetation characteristics such as dense understory and browse availability because they have an influence on hare density. However, there are other factors that influence how vegetation develops following a burn. For example, differences in fire severity (Johnstone and Kasischkhe 2005) and distance to seed source (Chapin et al. 2006) can cause the successional trajectory and species composition to vary among burns of the same age. These differences might influence the spatial and temporal differences in vegetation development, causing variation as seen in the young burns in this study. I recommend the use of distance to seed source and fire severity as covariates with TSLF to help explain patterns of hare density on the landscape.

Other suggestions to improve method performance are to (1) stratify transects to produce strata with more uniform hare densities (Buckland et al. 2001); (2) use density of understory vegetation as a covariate; (3) use habitat

specific decomposition rates estimated by the retrospective method (Laing et al. 2003); and (4) use species and season specific deposition rates.

Snowshoe Hares and Fire

Under forecast climate warming with increasing wildfire activity and area burned (Starfield and Chapin 1996; Rupp et al. 2000), the amount of deciduous vegetation will likely increase and average stand age will become younger. An insight into how these changes might affect the inhabitants of the boreal forest will be important in understanding a changing ecosystem.

An increase in fire activity could influence the average hare density on the landscape in 2 ways. First, an increase in deciduous vegetation with a reduction in average stand age could increase the landscape's carrying capacity for snowshoe hares through a higher availability of high quality browse. Second, an increase in the number of fires each year can lead to a patchier landscape as large areas of uniform mature black spruce are broken-up by early successional post-burn vegetation. Increased landscape patchiness and high food availability could increase the landscape's potential for hare density at both cyclic peaks and lows. This new mosaic could allow snowshoe hares to shift habitats depending on seasonal demands of food quality and escape cover as described by Wolff's (1980) refugium model.

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Figures

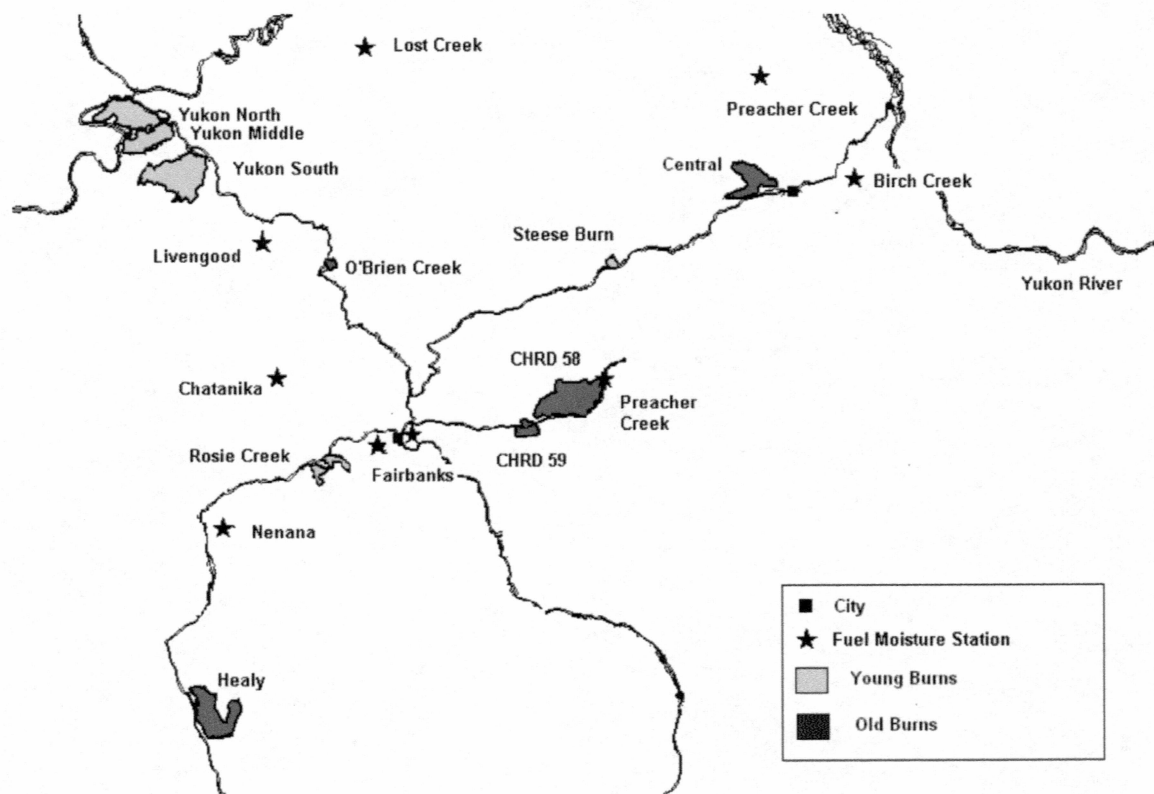


Figure 1. Map over the study area showing location of study sites and fuel moisture stations.

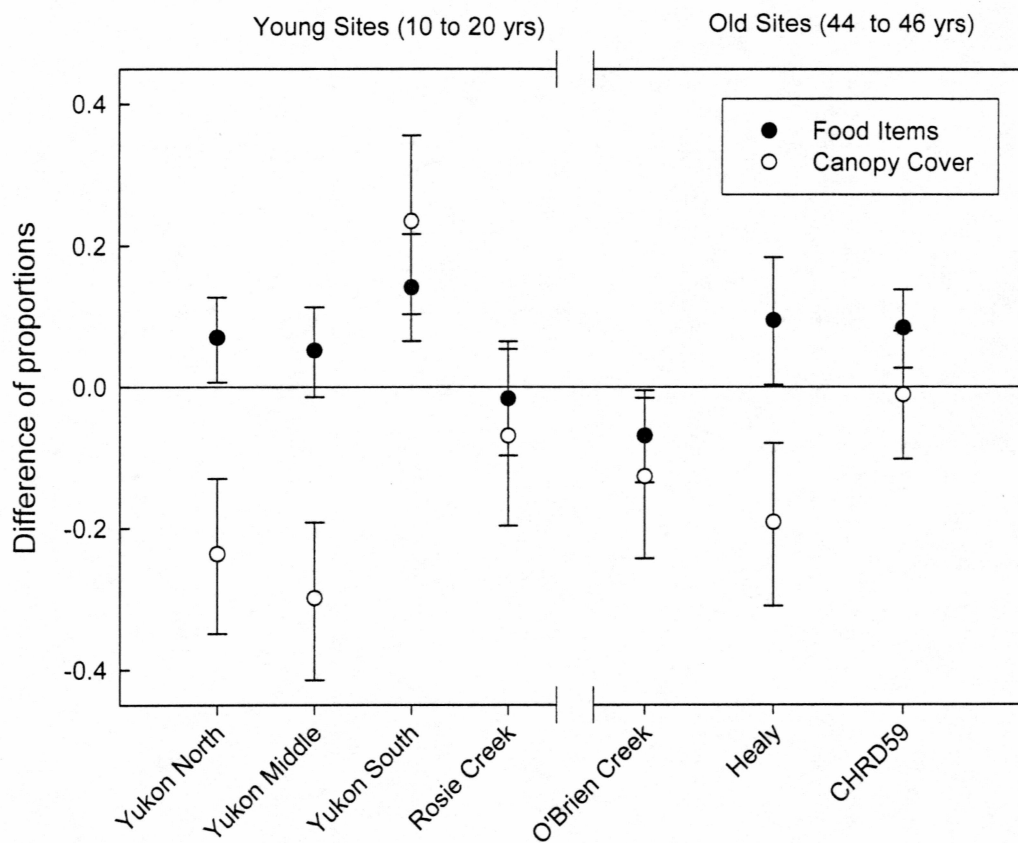


Figure 2. The difference in proportions of browse and canopy cover between burned and control areas, respectively. A positive difference indicates a higher proportion in the burn. Error bars are 95% confidence intervals

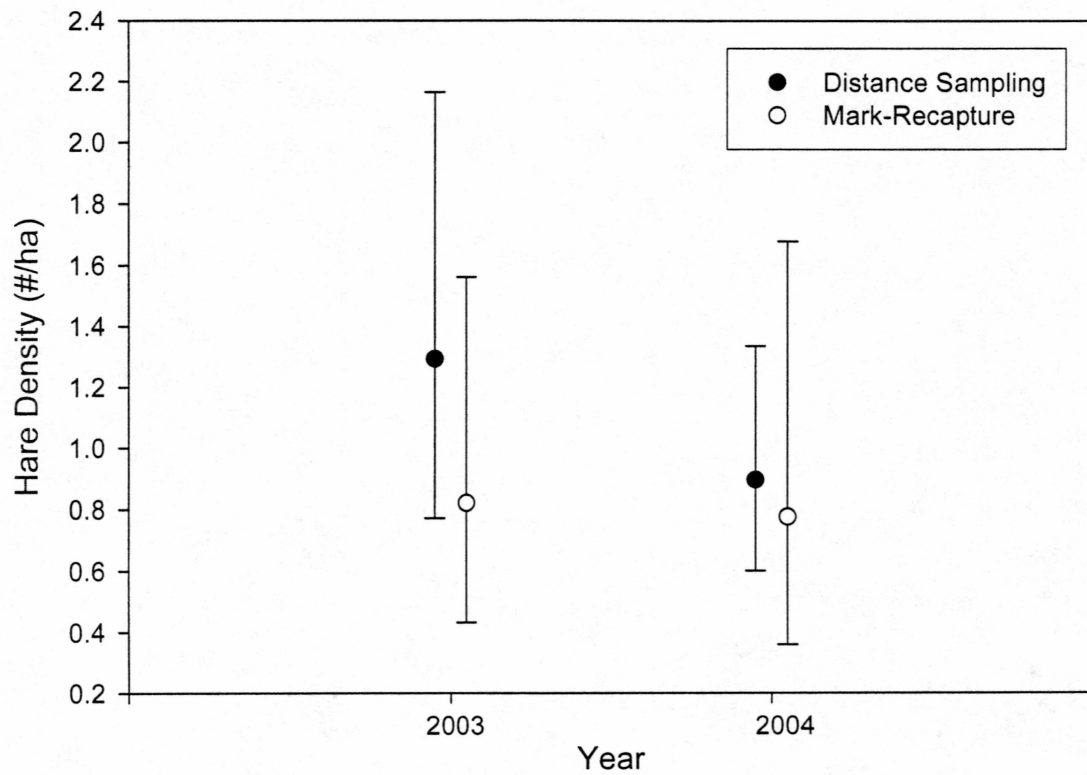


Figure 3. Snowshoe hare densities as estimated from indirect distance sampling and direct mark-recapture in August of 2003 and 2004. Error bars are 95% confidence limits.

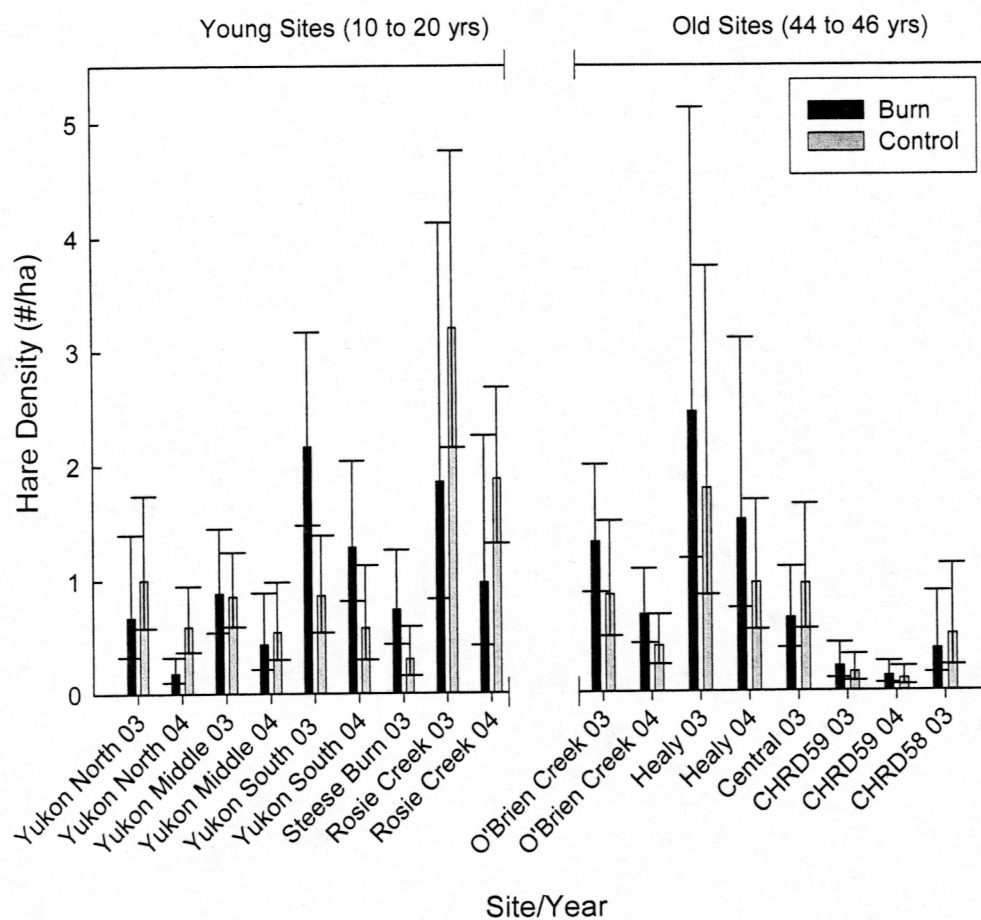


Figure 4. Hare densities ordered by site and year. Error bars are 95% confidence intervals.

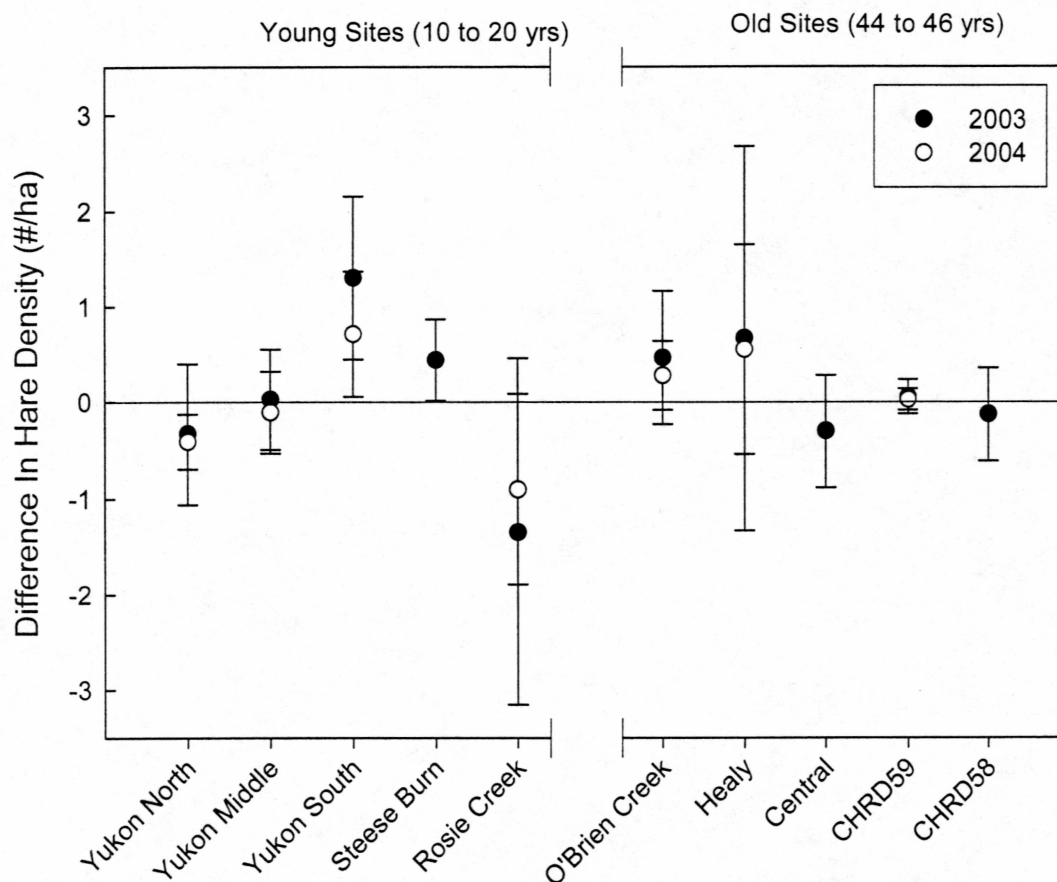


Figure 5. The difference in snowshoe hare density is between burned and control areas within sites. A positive difference indicates higher hare density in the burn. Error bars are 95% confidence intervals.

Tables

Table 1. Name of the burned areas, year the area burned and the size in hectares of the burns used in the study.

Burn Name	Year	Hectare	UTM Coordinates*
Yukon North	1993	15460	06w0382500 7301500
Yukon Middle	1990	10965	06w0386400 7297666
Yukon South	1991	22654	06w0399464 7286855
Steese	1990	740	06w0537843 7249166
Rosie Creek	1983	2771	06w0447000 7185555
O'Brien Creek	1958	1064	06w0441600 7249629
Central	1957	9914	06w0585140 7272800
Healy	1958	15889	06w0397250 7099438
CHRD 58	1958	58881	06w0519300 7198850
CHRD 59	1959	3276	06w0509270 7194350

* UTM Coordinates indicate the starting point of the 1st transect in the burn.

Table 2. Proportions of total canopy cover (a) and proportions of relative availability of browse (b) in burned and unburned areas.

Canopy Cover	2a		CHRD 59		Old Sites Healy		O'Brien Cr.		Rosie Cr.		Yukon Middle		Young Sites Yukon South		Yukon North	
	Area	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Control
	P	0.530	0.542	0.180	0.372	0.475	0.602	0.522	0.592	0.344	0.642	0.628	0.393	0.331	0.567	
	X	174	104	22	45	67	103	71	71	67	77	76	48	84	68	
	N	328	192	122	121	141	171	136	120	195	120	121	122	254	120	
	Z _c	0.156		3.198		2.131		0.992		5.041		3.530		4.224		
	P-value	0.438		P<0.001		0.017		0.161		p<0.001		p<0.001		p<0.001		
Browse	2b		CHRD 59		Old Sites Healy		O'Brien Cr.		Rosie Cr.		Yukon Middle		Young Sites Yukon South		Yukon North	
	Area	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Control
	P	0.308	0.224	0.557	0.479	0.17	0.24	0.283	0.3	0.210	0.158	0.293	0.152	0.224	0.154	
	X	202	86	140	116	48	82	77	72	82	38	71	37	114	37	
	N	656	384	244	242	282	342	272	240	390	240	242	244	508	240	
	Z _c	2.849		1.631		2.030		0.323		1.507		3.649		2.137		
	P-value	0.002		0.051		0.021		0.373		0.066		p<0.001		0.016		

Note: Proportion (P) of recorded "hits" (X) with the densitometer over the total number of samples (N), Z_c is the test statistic, P-value is based on the comparison between burned and unburned canopy cover

Table 3. Average Fine Fuel Moisture Code (FFMC) and their standard errors for weather stations in interior Alaska.

Year	Station	Mean	S.E.
2003	Fairbanks	67.24	3.0
	Fairbanks Airport	69.44	2.41
	Angel Creek	64.73	3.12
	Birch Creek	79.06	2.24
	Caribou Peak	57.96	3.49
	Chatanika	56.83	3.31
	Livengood	70.09	2.6
	Preacher Creek	74.74	2.02
2004	Fairbanks	86.11	1.16
	Fairbanks Airport	85.78	0.96
	Angel Creek	86.62	1.31
	Birch Creek	87.39	1.09
	Caribou Peak	82.88	1.64
	Chatanika	83.49	1.39
	Livengood	86.33	1.15
	Lost Creek	89.05	0.54
	Nenana	83.87	1.05
	Preacher Creek	88.06	0.99

Note: The averages are calculated from daily readings from 2 July - 30 September in 2003 and 3 June – 1 September in 2004.

Table 4. Meta-analysis of the hare density between burn and control.

	2003						2004					
	\hat{d}_i	$\text{var}(\hat{d}_i)$	Weight $1/\text{var}(\hat{d}_i)$	Group weighted mean	Group variance	P-value	\hat{d}_i	$\text{var}(\hat{d}_i)$	Weight $1/\text{var}(\hat{d}_i)$	Group weighted mean	Group variance	P-value
Yukon North	-0.332	0.139	7.192				-0.413	0.021	47.374			
Yukon Middle	0.027	0.071	13.993				-0.108	0.047	21.133			
Yukon South	1.3	0.189	5.282	0.257	0.065		0.711	0.112	8.954	-0.234	0.048	
Steese	0.439	0.047	21.094						N/A			
Rosie Creek	-1.347	0.851	1.175				-0.904	0.255	3.922			
O'Brien Creek	0.465	0.127	7.883			0.205	0.278	0.034	29.511			0.103
Healy	0.671	1.041	0.96				0.554	0.314	3.19			
Central	-0.304	0.088	11.326	0.032	0.006				N/A	0.053	0.004	
CHRD 59	0.052	0.008	118.74				0.026	0.003	297.076			
CHRD 58	-0.128	0.061	16.271						N/A			

Note: \hat{d}_i = difference in hare density, $\text{var}(\hat{d}_i)$ is the variation of the difference, Weight is the inverse of the variance.

Table 5. The percentages of the variance of hare density estimates explained by each of the contributing variables.

Site	Area	Detection Probability		Encounter Rate		Pellet group Disappearance Rate		Pellet group Production Rate	
		2003	2004	2003	2004	2003	2004	2003	2004
Yukon	Burn	18	20	72	70	4	3	7	7
North	Control	45	26	36	57	7	6	12	11
Yukon	Burn	23	16	54	77	9	2	14	5
Middle	Control	19	9	42	80	15	4	24	7
Yukon	Burn	12	8	48	72	16	7	25	13
South	Control	23	43	51	49	10	3	16	5
Steese	Burn	20	N/A	60	N/A	8	N/A	13	N/A
	Control	20		67		5		8	
Rosie	Burn	7	7	83	87	4	2	6	4
Creek	Control	13	24	50	46	14	10	23	20
O'Brien	Burn	30	16	38	66	13	6	20	12
Creek	Control	19	25	62	61	7	4	12	9
Healy	Burn	2	4	85	88	5	3	8	5
	Control	4	12	83	75	5	4	8	9
Central	Burn	25	N/A	53	N/A	8	N/A	13	N/A
	Control	15		64		8		13	
CHRD	Burn	18	23	69	69	5	2	8	5
59	Control	0	0	86	92	6	3	9	5
CHRD	Burn	0	N/A	91	N/A	4	N/A	6	N/A
58	Control	23		68		4		6	

Conclusions

The hare density estimates from this study are higher than for most other cyclic low estimates of hare density from other parts of the northern boreal forest (Table 6.1 in Hodges 2000a). However, Murray et al. (2002) reported snowshoe hare density estimates of up to 2.12 hares/ha from low-density populations, which is in the range of hare density estimates from this study (2004: 0.2 to 2.5 hares/ha).

A comparison of sampling methods showed no significant difference between the indirect and the direct sampling strategies. These results indicate that distance sampling of fecal pellet groups can be as effective as mark-recapture methods in estimating hare density.

The results from this study indicate that young burns in contrast to old burns are more variable in their influence on hares. It is possible that many of the burns included in the young age category had either not yet developed the vegetation structure that influence hare density, or had passed the successional stage where they are attractive to hares.

I used TSLF as a proxy for vegetation characteristics such as dense understory and browse availability because they have an influence on hare density. However, there are other factors that influence how vegetation develops following a burn. For example, differences in fire severity (Johnstone and Kasischke 2005) and distance to seed source (Chapin et al. 2006) can cause

the successional trajectory and species composition to vary among burns of the same age. These differences might influence the spatial and temporal differences in vegetation development, causing variation as seen in the young burns in this study. I recommend the use of distance to seed source and fire severity as covariates with TSLF to help explain patterns of hare density on the landscape.

Other suggestions to improve method performance are to (1) stratify transects to produce strata with more uniform hare densities (Buckland et al. 2001); (2) use density of understory vegetation as a covariate; (3) use habitat specific decomposition rates estimated by the retrospective method (Laing et al. 2003); and (4) use species and season specific deposition rates.